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ON THE RISK OF EXTINCTION

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A major problem in population biology is to understand what determines the expected lifetime (or, alternatively, the risk of extinction) of a population. Understanding this risk is of theoretical interest to population biologists, but it is a central practical issue for conservation biologists and wildlife managers concerned with saving populations.

Even in a perfectly constant environment, small populations face appreciable risk from demographic accidents, the vagaries of birth and death schedules and of sex-ratio fluctuations. In practice, the environment does fluctuate, and this superimposes an additional risk of extinction on that arising from demographic accidents alone. Finally, even large populations may be destroyed by some extraordinary perturbation, such as the total logging of a forest. Clearly, there is a continuum, with different populations facing little to extreme environmental perturbation.

It is intuitively obvious that the risk of extinction is greater for populations consisting of a few individuals than for those having many, and it is greater for populations whose densities are subject to large variations through time than for populations with low temporal variability. Other things being equal (which they are not!), a population of a long-lived species would have a lower risk of extinction per year than would a short-lived species. Moreover, populations with a low intrinsic rate of increase, r , clearly should be at increased risk of extinction, because they would recover slowly from a severe reduction in density and thus remain longer at risk of extinction from demographic accidents.

The ideas of the preceding two paragraphs are condensed from several mathematical models (MacArthur and Wilson 1967; Richter-Dyn and Goel 1972; Leigh 1975, 1981; Goodman 1987). Our first objective in this paper is a more complete theoretical exploration of these ideas, in order to predict how the risk of extinction varies between species.

Data for testing these predictions must include numerous observations of extinctions under relatively "normal" conditions. By "normal," we mean extinctions not clearly attributable to man's destructive influences. The data should be

for many species with different numbers of individuals, temporal coefficients of variation, and life histories. A suitable data base (Appendix) consists of the repeated annual breeding censuses of British island birds, already analyzed in studies of species turnover (Lack 1969; Diamond and May 1977; Williamson 1983; Diamond 1984a). For 16 islands around Britain, the numbers of breeding pairs of all land-bird species have been determined in many consecutive years for up to several decades. Some populations become locally extinct and others are founded. The islands vary in area, the populations are of various sizes and temporal variabilities, and the species have various life histories.

In an analysis of these data (Diamond 1984a), the effect of population size on extinction rate was overwhelming, as predicted. In addition, populations of a given size varied significantly in their extinction rates. Is such variability merely noise, or does it reflect predictable differences between species? Comparing species across islands, these analyses show that certain species tended to deviate consistently from the average: some species were prone to extinction, whereas others were relatively immune. Hence, our second objective is to explore these interspecific differences, using as a guide the theoretical insights derived in the first part of our paper.

Our analysis of the British island-bird data is more extensive than this earlier analysis (Diamond 1984a) in four respects. First, we adjust the extinction rate for population size. We can therefore analyze extinction rates of different-sized populations of different species and extract the interspecific component of differences in extinction rate, independent of population size. Second, we recall that body size is closely linked with both longevity and intrinsic rate of increase, which have opposite effects on extinction rates. We show that the effect of body size on extinction rate is both more interesting and more complex than previously recognized. In particular, we expect theoretically, and confirm empirically with the bird data, that, for a given population size, large species have a lower risk of extinction than small species when the mean population size is relatively small, but a higher risk of extinction when the population sizes are large. Third, we confirm the theoretical prediction that populations whose densities vary more through time are more prone to become extinct than are less variable populations. Fourth, we find that species that migrate are more prone to extinction than species that remain on or near the islands.

THEORY

To introduce the theory, we first examine the factors that cause population change and then examine how species with different life histories will respond to these factors.

Demographic Accidents and Environmental Disturbances

Consider two extreme cases. In the first case, extinction is caused solely by demographic accidents in an unvarying environment. Models of this case assume constant per capita birth and death rates up to some population ceiling, K , above which the birthrates are assumed to be zero. These models predict very rapid

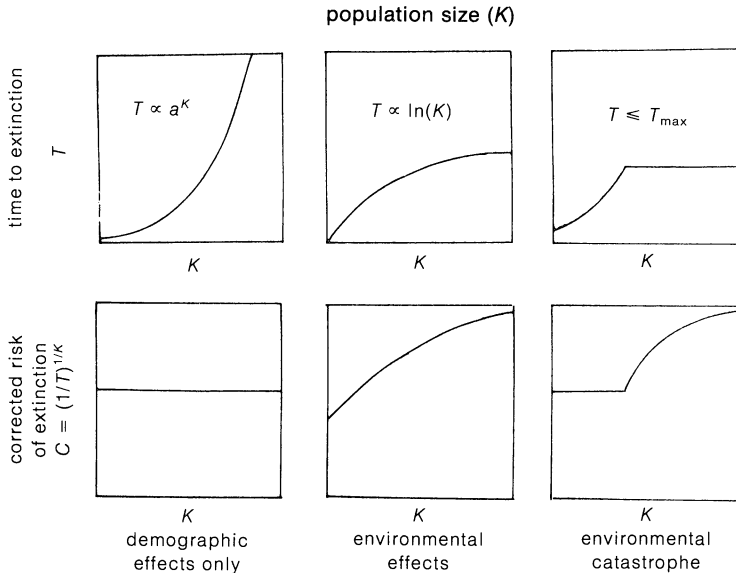


FIG. 1.—Times to extinction (T , above) and corrected risk of extinction ($C = (1/T)^{1/K}$, below) for models of three different sources of extinction: *left*, for extinctions resulting only from demographic accidents in an unvarying environment, T increases approximately as the power of maximum population size (K), such that C is independent of K ; *center*, in Leigh's (1981) model that considers both demographic effects and moderate environmental variation, T increases as the logarithm of K ; *right*, for environmental catastrophes that strike after a time T_{\max} and destroy all surviving populations, no population survives beyond T_{\max} (but some small populations might die out before the catastrophe; hence, the kink in the line). T increases much more steeply with K if demographic effects predominate than if effects of environmental variation predominate. C shows less-extreme dependence on K than does T .

increases in times to extinction (T) as K increases. Goodman (1987) pointed out that for MacArthur's (1972) model, T increases approximately as a constant to the power K (i.e., T scales as a^K : fig. 1, upper left).

For the opposite extreme case, consider the ultimate form of external environmental disturbance, total destruction of the habitat, such as might result from logging of a forest or an asteroid collision or a nuclear holocaust. The time to extinction will be the same for all species, irrespective of population size, provided that this time is less than the time expected in the absence of the disturbance.

The first case is not unrealistic, and the second case is, we hope, avoidable, but the cases demonstrate an important point. For demographic accidents alone, time to extinction increases rapidly with population size. For a given population size, environmental variation reduces the time to extinction below that expected from demographic accidents alone in an unvarying environment. As environmental variability increases, the increase in time to extinction with population size becomes more modest, reaching our extreme case (of no increase at all) when environmental disasters are catastrophic. Leigh (1981) suggested that, under some

kinds of environmental disturbance, the time to extinction may increase with the logarithm of K (fig. 1, upper left), and one of Goodman's (1987) models has the time to extinction increasing more slowly than the square of the logarithm of K . This rate is much slower than a^K , the dependence expected from demographic accidents alone.

We obtain a more convenient way of expressing these conclusions if we consider two quantities. We call the first the risk of extinction, $1/T$. Its behavior under the different models follows from what we have discussed in the previous paragraphs. Thus, when T increases at the rate a^K , $1/T$ quickly becomes very small as K increases. We base our statistical analyses on the second quantity, the corrected risk of extinction, C , which equals $(1/T)^{1/K}$. For cases in which the time to extinction increases with increasing a^K (e.g., demographic accidents only), C is independent of K . Similarly, C decreases with K if the time to extinction increases more rapidly than a^K , and C increases with K if T increases more slowly than a^K (fig. 1). Therefore, depending on which model of extinction we use, T may increase much more rapidly or slowly with K than with a^K , but the change in C with K is more modest. This behavior of C makes it useful for our analysis.

Species Responses

We have already mentioned three intuitively obvious theoretical results for how extinction times should vary among species. Extinction rates should be lower for species with (1) high intrinsic rates of increase (r), (2) high longevity, and (3) low temporal coefficients of variation in density (CV). The difficulty is that all three parameters are linked.

Rates of increase and longevity.—We are not able to provide estimates of longevity and rates of increase directly. However, both of these parameters correlate with body size, and body sizes are readily available. Across animal species from protozoans to elephants, an increase in r of one order of magnitude corresponds to an equal decrease in longevity. But both r and longevity are known empirically to be closely related to body size, in ways that have opposite effects on extinction rates. Large body size is associated with low r (Southwood 1981, p. 34), which tends to raise extinction rates (Leigh 1981; Goodman 1987). Large body size is also associated with high longevity (Bonner 1965, p. 17), which tends to lower yearly extinction rates. What is the net effect of body size on T ? Should we expect a small-bodied species with high r and a short lifetime to be more or less likely to become extinct than a large-bodied species with a correspondingly low r and a long lifetime? (We assume that both species have the same equilibrium density, of course.) We present two arguments, a general verbal argument and a more illustrative quantitative calculation, showing that the advantage of species with high r (which tend to be small-bodied) over species with low r (which tend to be large-bodied) holds only for relatively large population sizes.

For the verbal argument consider two extremes. First, consider single individuals of a large-bodied and a small-bodied species. Both are doomed to die, but the former will probably live longer; its yearly extinction rate is lower, even if the per-lifetime rates of extinction for the two species are the same. Second, consider identically sized large populations of the two species. The large-bodied species is

TABLE 1
TIMES TO EXTINCTION, IN LIFETIMES, DERIVED FROM A MODEL OF
LEIGH (1981, TABLE 2)

<i>r</i>	<i>K</i>			
	5	10	20	40
0.1	21	46	197	4877
0.2	25	109	2844	4.3×10^6
0.3	38	414	9.2×10^4	1.1×10^{10}
0.4	72	2312	5.2×10^6	5.8×10^{13}

NOTE.—In the model, the populations grow exponentially at rate r up to a density K , which they cannot exceed. There is an empirical negative correlation between longevity and r . Thus, individuals in a population with an r of 0.1 would be expected to live, on the average, four times as long, in years, as individuals in a population with an r of 0.4. Hence, a population with $r = 0.1$ and $K = 5$ should last slightly longer ($4 \times 21 = 84$ time units) than a population with $r = 0.4$ and $K = 5$ (72 time units). At all higher values of K , populations with higher r values are at a great advantage: for example, at $K = 10$, the population with an $r = 0.1$ would be expected to last $4 \times 46 = 184$ time units, but the $r = 0.4$ population would last 2312 time units.

at a disadvantage because, following some severe reduction in numbers, its lower intrinsic rate of increase makes it take longer than the small-bodied species to climb from low levels to higher numbers. Although the large-bodied species may persist longer at low densities than a small-bodied species, remaining at low levels greatly increases the risk of extinction; a large-bodied, slowly growing species may still be at low levels when the next severe reduction in numbers occurs. In most models of extinction, it is this effect that causes times to extinction to decrease so rapidly with increases in r , for species with the same equilibrium numbers. These two extreme cases show that large-bodied species have an advantage over small-bodied species at low densities and that the reverse is true at high densities. However, these verbal arguments do not tell us at what density the advantage switches.

If we look at the time to extinction measured in lifetimes, not years, small-bodied species always have an advantage because of their high r . Measuring extinction times in generations may be sensible for some applications, but conservationists' plans for managing species will be measured in years, not in the different generation times of different species. The year is not a biologically arbitrary unit of time. For many species, dispersal, and hence movement between isolated populations, occurs on a yearly cycle. Thus, years, not lifetimes, may be the appropriate measure of the time until a foundering population may be rescued by immigrants.

For an illustrative numerical example, we turn to Leigh (1981), who provided a calculation of the times to extinction of a population that grows exponentially at rate r up to a density K , which it cannot exceed. The population encounters only demographic accidents. Some of these calculations are provided by table 1, which

shows the marked effect of increases in time to extinction as r increases. At $K = 10$, the expected time to extinction in lifetimes at $r = 0.4$ (time = 2312 lifetimes) is 50 times that at $r = 0.1$ (46 lifetimes). Individuals of the population with $r = 0.1$, however, are likely to live four times as long as those in the more rapidly growing population. But the rapidly growing population still has a 50/4 or 12.5-fold advantage in the time to extinction measured in years.

Similar calculations for a population of $K = 5$ show that a higher rate of increase is not advantageous: it is offset by the shorter longevity, resulting in the population's lasting for similar times as measured in years (table 1). Below $K = 5$, the advantage shifts to the longer-lived populations with lower r .

Temporal coefficient of variation (CV) of population size.—Temporal variability of population size also depends on body size, r , and longevity. We might expect, despite some counterexamples, that large-bodied species would tend to survive an environmental disturbance better than small-bodied species. Yet, we have also argued that large, slowly growing species might recover more slowly from reductions in density than would small species with short reproductive cycles. Thus, body size affects not only the time to extinction but also CV in opposite ways. Should the net result be that large-bodied or small-bodied species have higher CV's?

For many of the British bird species that we discuss, we can document both the advantages and disadvantages of large body size. Hard winters are a major cause of abrupt population declines in British birds, and small-bodied species suffer greater proportional reductions in density during hard winters than do large-bodied species (Cawthorne and Marchant 1980). However, the major component of temporal variation in population densities comes from the slowness of recovery from these reductions. Species that recover slowly tend to have larger CV's than species that recover quickly; slowly recovering species spend longer at low densities (Pimm 1984). This results in a negative correlation of CV with the rate of increase, r : slowly growing populations have higher CV's, even given their more modest declines following a severe disturbance. Although CV and body size might thus have an overall negative correlation, this is not a strong effect: large-bodied species show much the same range of CV's as small-bodied species (Pimm 1984).

Summary of Theoretical Points

The preceding discussion can be summarized as four predictions. All other things being equal, extinction rates will be greater (1) in small populations than in large populations; (2) at low population densities, in small-bodied, fast-growing, short-lived species than in large-bodied, slow-growing, long-lived species; (3) at high population densities, in large-bodied, slow-growing, long-lived species than in small-bodied, fast-growing, short-lived species; and (4) in populations with high rather than low temporal CV's.

Point 1 has been predicted by several theoretical treatments (MacArthur and Wilson 1967; Richter-Dyn and Goel 1972; Leigh 1975, 1981; Goodman 1987) and confirmed by observations of many actual populations (for a summary, see Diamond 1984a). We now test the three remaining predictions.

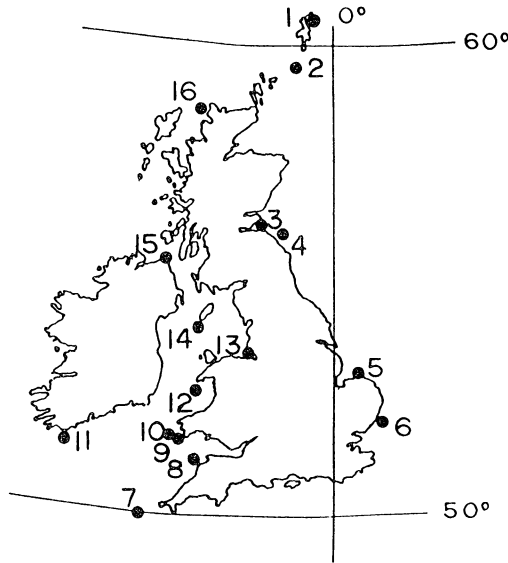


FIG. 2.—Locations of the 16 British islands used in this study. Numbers in parentheses are the island areas in square kilometers. 1, Hascosay (3.0); 2, Fair Isle (7.65); 3, Isle of May (0.49); 4, Inner Farne (0.29); 5, Scolt Head (3.34); 6, Havergate (1.08); 7, St. Agnes (1.09); 8, Lundy (4.52); 9, Skokholm (0.97); 10, Skomer (2.92); 11, Cape Clear (6.39); 12, Bardsey (1.8); 13, Hilbre (0.07); 14, Calf of Man (2.49); 15, Copeland (0.32); 16, Handa (3.10).

THE DATA BASE

Bird censuses compiled and evaluated by Timothy Reed were analyzed (Jones and Diamond). These censuses are for 16 islands off the coast of Britain, ranging in area from 0.07 to 7.65 km² (fig. 2, legend). Complete sets of censuses for several of the islands have been published elsewhere (Lack 1969; Diamond and May 1977; Diamond 1984*a,b*). The data consist of consecutive yearly counts of the number of nesting pairs of each land-bird species on an island (Appendix). The data sets for all 16 islands include 100 bird species and 355 populations (355 island-species combinations).

The species are diverse taxonomically and trophically. They include insectivores (swallows, martins, pipits, wagtails, warblers, and, while on the breeding grounds, many of the shorebirds); seed eaters (doves, finches, buntings); and carnivores (hawks, buzzards, falcons). Some of the species are residents, but others are migratory; we have indicated which in table 2.

For species that migrate from the island for the winter and return in the spring to breed, should we equate a breeding absence with a local population extinction? Banding studies have shown that at least some of the migratory species on British islands are philopatric: individuals return yearly to the same area to breed. Thus, when such a species that bred on an island one year fails to appear in the next year, this usually means that the individuals constituting the population died, not

TABLE 2

SPECIES, THEIR EXTINCTION CHARACTERISTICS, THEIR SIZES, WHETHER THEY MIGRATE, AND THE VARIABILITY OF THEIR POPULATION DENSITIES

Species	1/T	N	CV	C	Size	MS	Residual
Sparrowhawk	0.330	1.000		0.3200	L	R	-0.062
Buzzard	0.183	2.000	0.23	0.4278	L	R	-0.018
Kestrel	0.244	1.210	0.17	0.3117	L	R	-0.084
Peregrine	0.595	1.125	0.33	0.6303	L	R	0.240
Grey partridge	0.113	5.167	0.68	0.6557	L	R	0.011
Quail	0.670	1.000		0.6700	L	M	-0.025
Red-legged partridge	0.130	2.750		0.4762	L	R	-0.016
Pheasant	0.260	5.630	0.35	0.7872	L	R	0.113
Water rail	0.060	3.000		0.3915	L	R	-0.116
Corncrake	0.237	4.670	0.70	0.7347	L	M	0.035
Moorhen	0.123	4.056	0.44	0.5965	L	R	0.021
Coot	0.200	1.000	0.00	0.2000	L	R	-0.182
Lapwing	0.137	6.960	0.58	0.7516	L	M	0.049
Golden plover	1.000	1.670		1.0000	L	M	0.304
Ringed plover	0.037	5.560	0.43	0.5527	L	R	-0.116
Curlew	0.322	2.830	0.35	0.6700	L	M	-0.028
Redshank	0.250	4.375	0.46	0.7284	L	M	0.029
Snipe	0.062	4.125	0.26	0.5096	L	M	-0.190
Stock dove	0.287	3.670	0.34	0.7117	L	R	0.161
Rock dove	0.027	8.330	0.18	0.6482	L	R	-0.195
Wood pigeon	0.137	2.750		0.4854	L	R	-0.007
Cuckoo	0.396	1.430		0.5232	L	M	-0.173
Short-eared owl	0.242	2.000	0.70	0.4919	L	R	0.046
Little owl	0.500	2.750	0.27	0.7772	L	R	0.285
Magpie	0.100	4.500	0.46	0.5995	L	R	-0.003
Jackdaw	0.375	7.120	0.28	0.8713	L	R	0.104
Carrion crow	0.218	4.580	0.24	0.7171	L	R	0.110
Raven	0.017	2.350	0.30	0.1766	L	R	-0.291
Skylark	0.031	6.870	0.41	0.6031	S	R	-0.111
Swallow	0.389	3.830	0.41	0.7815	S	M	-0.042
House martin	0.463	5.000		0.8573	S	M	0.059
Yellow wagtail	1.000	1.250		1.0000	S	M	0.120
Pied wagtail	0.337	2.270	0.28	0.6193	S	R	-0.130
Meadow pipit	0.105	5.350	0.41	0.6562	S	R	-0.070
Wren	0.090	8.700	0.62	0.7582	S	R	0.058
Dunnock	0.137	6.100	0.41	0.7219	S	R	0.002
Robin	0.250	3.330	0.26	0.6595	S	R	-0.082
Stonechat	0.420	3.640	0.49	0.7879	S	R	0.049
Wheatear	0.383	4.830	0.33	0.8198	S	M	0.018
Blackbird	0.307	4.670	0.44	0.7766	S	R	0.045
Song thrush	0.588	1.700		0.7317	S	R	-0.022
Mistle thrush	0.557	1.330		0.6440	S	R	-0.113
Grasshopper warbler	0.835	1.000		0.8350	S	M	-0.050
Sedge warbler	0.314	1.900		0.5435	S	M	-0.322
Whitethroat	0.440	4.420	0.48	0.8305	S	M	0.019
Willow warbler	0.900	1.250		0.9192	S	M	0.040
Chiffchaff	1.000	1.000		1.0000	S	M	0.115
Goldcrest	1.000	1.000		1.0000	S	R	0.241
Spotted flycatcher	0.813	1.000		0.8130	S	M	-0.072
Great tit	0.165	2.500	0.35	0.4864	S	R	-0.261
Blue tit	0.315	1.500		0.4630	S	R	-0.292
Yellowhammer	0.500	2.500	0.38	0.7579	S	R	0.010
Reed bunting	0.197	5.630	0.67	0.7493	S	R	0.025
Chaffinch	0.517	2.370	0.42	0.7570	S	R	0.008

TABLE 2 (Continued)

Species	1/T	N	CV	C	Size	MS	Residual
Goldfinch	0.670	1.500		0.7657	S	R	0.010
Redpoll	1.000	1.000		1.0000	S	R	0.241
Linnet	0.196	6.500	0.44	0.7782	S	R	0.061
House sparrow	0.333	4.500	0.27	0.7832	S	R	0.051
Tree sparrow	0.527	2.170		0.7444	S	R	-0.006
Starling	0.024	11.620	0.41	0.7254	S	R	0.047
Pied flycatcher	1.000	1.000		1.0000	S	M	0.115
Siskin	1.000	1.000		1.0000	S	R	0.241

NOTE.—The scientific names of the species are given in the Appendix. $1/T$ is the risk of extinction, the mean of the reciprocal times to extinction for each species, averaged over all the islands on which that species occurred. Species that did not become extinct on any island are not included. Species that did not become extinct on certain islands were assigned $1/T$ values of zero for those islands. N is the mean number (across all the islands on which the species occurred) of the mean number of nesting pairs (over all the years when the species was present). CV is the mean coefficient of variation of numbers of nesting pairs over time, across all the islands on which the species persisted for five or more years. C is the "corrected risk of extinction" defined as $(1/T)^{1/N}$. Size is L (large) for non-passerines and corvids, S (small) for other species. MS, migrant status, is R for resident species, M for migrant species. Migrant species include both migrants that fly to Africa or southern Europe for the winter and those species which, like many of the shorebirds that may remain in Britain, use different habitats or islands in the winter. Residuals are the deviations of the values of C from the statistical models presented in table 3 and shown graphically in figure 4. Positive values indicate that the species is more likely to become extinct than would be expected on the basis of the species' population density and body size.

that they merely moved elsewhere to breed. When and if the island is recolonized, it will be by different individuals.

There are several reasons why migratory and resident species might be expected to differ in their susceptibility to extinction. First, some individuals of migratory species (even of ones that are usually philopatric) probably go one year to a breeding area that was not their breeding area the preceding year. If these individuals were from an island, their wandering might cause a local extinction. Alternatively, by wandering from the mainland in one year, they might establish a short-lived island population. In either case, the migrants would appear more prone to extinction than residents. Second, migrants and residents might also be expected to differ in the variability of their densities. On the one hand, migrants avoid the unusually hard winters that depress resident bird populations. On the other hand, migration itself is risky. The net result is that the densities of migratory species are marginally more variable than those of resident species (Pimm 1984). Because of these considerations, we analyzed the difference between migrants and residents in their risk of extinction, but we could not predict *a priori* which group would be at greater risk.

Data Preparation

For each population, we recorded the mean number of nesting pairs for the years in which that species actually bred on that island (Appendix, col. 4). For each species, we then calculated a mean (averaged over all the islands on which

the species bred) of the mean numbers of nesting pairs on each island; the means of the means are abbreviated N (table 2, col. 3).

We calculated the coefficient of variation (CV) of the number of nesting pairs (Appendix, col. 5) for each population for which there were five or more years of continuous breeding. (Hence, we did not calculate CV's for many populations that bred for only short periods. However, we did calculate coefficients for populations whose mean density exceeded 18 pairs and which, as discussed below, are excluded from our calculation of risk of extinction.) The calculation included only years in which the species bred; zero density values were excluded. (To include all these zero values would greatly inflate the coefficients for populations that became extinct, making it much more likely that we would find a correlation between the chance of extinction and temporal variation. Expressed alternatively, one cannot calculate a CV of a population that no longer exists.)

For each species, we then calculated a mean CV (table 2, col. 4), by averaging over all islands for which the CV had been calculated. Reliable values of CV were available for 39 species of table 2.

For each population, we also recorded the number of years that it lasted, that is, the consecutive number of years of breeding, from immigration to extinction. Some populations repeatedly became extinct on a given island and then returned, yielding several values for the number of years that they survived. To extract the greatest amount of information from these data poses a considerable statistical challenge, as discussed below. We first outline our methods of processing these times that species survived on each island, and then in the next section ("Technical Comments") we justify these particular methods.

First, we calculated the reciprocal of the number of years that each population survived (Appendix, col. 3). This reciprocal was taken as zero for the many populations that survived without extinction for the entire sequence of census years. We excluded populations with a mean number of nesting pairs greater than 18, since 18 pairs was the highest mean number for which an extinction was recorded; this left 316 populations of 67 species. For each species, we then calculated a mean reciprocal time to extinction (abbreviated $1/T$; table 2, col. 2) by averaging over all islands the reciprocals of the number of years survived on each island. $1/T$ has units of year^{-1} , and we call it risk of extinction per year. Only species (62 in all) for which at least one extinction was recorded are included in table 2. Five species (occurring on 1, 2, 2, 4, and 9 islands) had average densities of less than 18 pairs but still did not become extinct during the period they were counted. We show below that including these species leaves our conclusions unaltered.

Maximum population size, K , is a theoretical construct, and real populations may not have such a fixed ceiling; moreover, it is not readily measurable in the field. What we can measure in the field is the average population size, N ; it closely correlates with K in the models. The risk of extinction per year must depend heavily on population size, N . In order to remove as much of this dependence as possible and thus observe how the risk of extinction depends on factors other than population size, we calculated for each species what we call the corrected risk of extinction, C (table 2, col. 5), as $C = (1/T)^{1/N}$. C is independent of N if the time to

extinction increases as a constant to the power N . Thus, C represents a species-specific risk of extinction, corrected for species differences in mean population size.

As a dichotomous expression of body size (table 2, col. 6), we categorized species as either "large" (non-passeriform birds, plus the large-bodied passerine family Corvidae: crows and ravens) or "small" (passeriform birds other than Corvidae). The two groups are divided by body size: birds with weights of 100–1000 g were "large" species, with only one exception (ringed plover, 65 g); birds of 5–100 g were "small" species, also with one exception (mistle thrush, 120 g).

Technical Comments

Our choices of methods require some comment because they involve some technical decisions.

1. We based our analysis on the statistic C , rather than on times to extinction, T , for two related reasons. First, the various theoretical models of extinction yield widely different relationships between T and population size, K (fig. 1). Even transforming T (e.g., by taking logarithms) may be inappropriate if T increases much faster or much more slowly than a constant to the power K . In contrast, changes in C should be more moderate. Second, and more important, the transformation from T to C leads to data that are approximately normally distributed with a common variance about the regression models that we develop. Other transformations do not achieve this.

2. Taking the reciprocals of T permits the inclusion of populations that did not become extinct during the course of the censuses; we take $1/T$ as zero for such populations. For a 30-yr series of censuses during which there was no extinction, we know only that T is between 30 and infinity. Yet to exclude such an observation from our analysis would cause a loss of many valuable observations: if our hypothetical population only had a mean population size of two pairs but suffered no extinction, its long-term persistence at that level would be remarkable. This reciprocal ($1/T$) in our example varies from only 0.033 to 0 and is thus statistically better behaved than T itself.

3. Despite the arguments of the preceding paragraph, we excluded populations that had average densities of more than 18 pairs, the density above which no species in our data became extinct. For many of the relatively abundant populations, no extinctions are recorded: what should be their value of C ($= (1/T)^{1/N}$)? To make the values of C zero for such species is misleading. To explain the reason for this, notice that an observation of no extinction over, say, 20 yr can be either remarkable or not, depending on the average density of the species over that time. As we argued in the preceding paragraph, if this density is only 2 pairs, the observation implies that the species is very resistant to extinction. But if that average density is as high as 30 pairs, the observation tells us virtually nothing about the species' susceptibility to extinction. A density of 30 pairs would permit species with a very wide range of risks of extinction to last 20 yr. If we were to assign C , the corrected risk of extinction, a value of zero for all those species in which no extinctions occurred, we would be forcing abundant species to appear intrinsically immune to extinction, regardless of their population size.

Simply expressed, the absence of extinctions grades from being informative at low densities to being uninformative at high densities. The obvious strategy is to exclude data at densities too high for us to observe extinctions.

4. A related argument motivates our method of handling the species that had densities below 18 pairs. We estimated C from the mean $1/T$'s and mean N 's, instead of calculating individual C 's for each population and taking their means. Furthermore, as already noted, we included only species that had at least one extinction.

To understand why this method works, consider two populations of the same species of the same average density. One lasted 10 yr, and its extinction was recorded. The other population lasted 11 yr, but we counted only birds on the island for 10 yr and thereby missed the extinction. The true values of C are very similar. Our method is to calculate the average of the reciprocal times to extinction, assigning zero to populations whose extinction we did not observe; hence, the values are $1/10$ and 0, and their average is 0.05. Consider what happens to the estimate of C as the average density of the two species increases. The estimate of C from this average is poor at low densities, but it quickly approaches the true value obtained from the true values of the reciprocals ($1/10$, $1/11$) as the density increases. We are likely to have many more data at low densities because there are going to be more extinctions at low densities, and this helps offset the errors in the estimates.

The alternative is to estimate C as the average of the two C values, the second of which we assign to zero. This method gives an estimate that gets progressively worse as density increases; yet we have the fewest extinctions at high densities. Simply expressed, errors at high densities are going to be harder to correct.

The problem with our method is that it excludes species for which we record no extinctions even though their average densities were small. We know that to report their C values as zero would be a serious underestimation of the values. These C values of zero would be expected to be outliers in a statistical analysis, as indeed they prove to be. But if we exclude such species and they comprise a substantial fraction of our populations, our results will be biased by our excluding species that are quite resistant to extinction. In fact, such species constitute only 5 of 67 species. We examine them separately in the "Results" section and show that they support our conclusions.

Statistical Analyses

For analyzing the C values, we used an analysis of covariance (ANCOVA) to investigate the dependence of C on population size for large and small species independently. The residuals about this statistical model were then regressed against the coefficients of variation (CV) of 39 species.

In the ANCOVA, the dependent variable C is $(1/T)^{1/N}$ and the independent variable is N . This presents a statistical dilemma, for N is present in both dependent and independent variables. Normally, we might analyze $1/T$ or some other function of T in terms of N and thereby separate the dependent from the independent variables. An obvious transform would be T or its logarithm. If we do this for our data, the pattern of variation deviates from the normal, independent variation of

TABLE 3
STATISTICAL ANALYSES

EFFECT	ANALYSIS OF COVARIANCE		
	<i>F</i>	<i>P</i>	<i>C</i>
ANALYSES OF THE CORRECTED RISK OF EXTINCTION			
Migrants			
Density	2.58	NS	
Density \times body size	0.32	NS	
Large-bodied			0.694 + 0.001 (density)*
Small-bodied			0.907 - 0.022 (density)*
Residents			
Density	29.49	<0.0001	
Density \times body size	8.13	0.001	
Large-bodied			0.32 + 0.063 (density)†
Small-bodied			0.767 - 0.008 (density)*
ANALYSIS OF RESIDUALS			
Coefficient of variation	3.47	0.05	
Body size	0.83	NS	
Migrants vs. residents	0.35	NS	
Residuals			-0.87 + 0.21 (coefficient of variation)‡

* Slope does not differ from zero.

† Slope differs from zero at $P = 0.0003$.

‡ Slope exceeds zero at $P < 0.05$.

uniform variance required for statistical inference. In contrast, the residual variation about our models for C does not deviate in this way.

Although our analysis is thus not completely satisfying, it is nevertheless justified for our purposes because of the following consideration. Our analysis is concerned with species differences, not with the exact relationship between C and N . Since all the data are subject to the same bias imposed by our regressing $(1/T)^{1/N}$ against N , differences in the relationships over the same range of N involving the same sample sizes must represent differences between species. It is about these differences between large- and small-bodied species that we wish to draw conclusions. These conclusions are unlikely to be affected by our failure to separate variables, because our data involve almost identical ranges of densities for large- and small-bodied species and nearly equal sample sizes (see figs. 3–5).

RESULTS

The results of our analyses are graphed in figures 3–5, and table 3 provides a summary of the associated statistical analyses. We consider, in turn, the effect of population size, effects related to body size, the effect of migration or its absence, and the effect of temporal coefficient of variation (CV).

Effect of Population Size

Figure 3 depicts the overwhelming dependence of the risk of extinction $(1/T)$ on population size (N). The risk of extinction decreases steeply with N , from 0.2 to

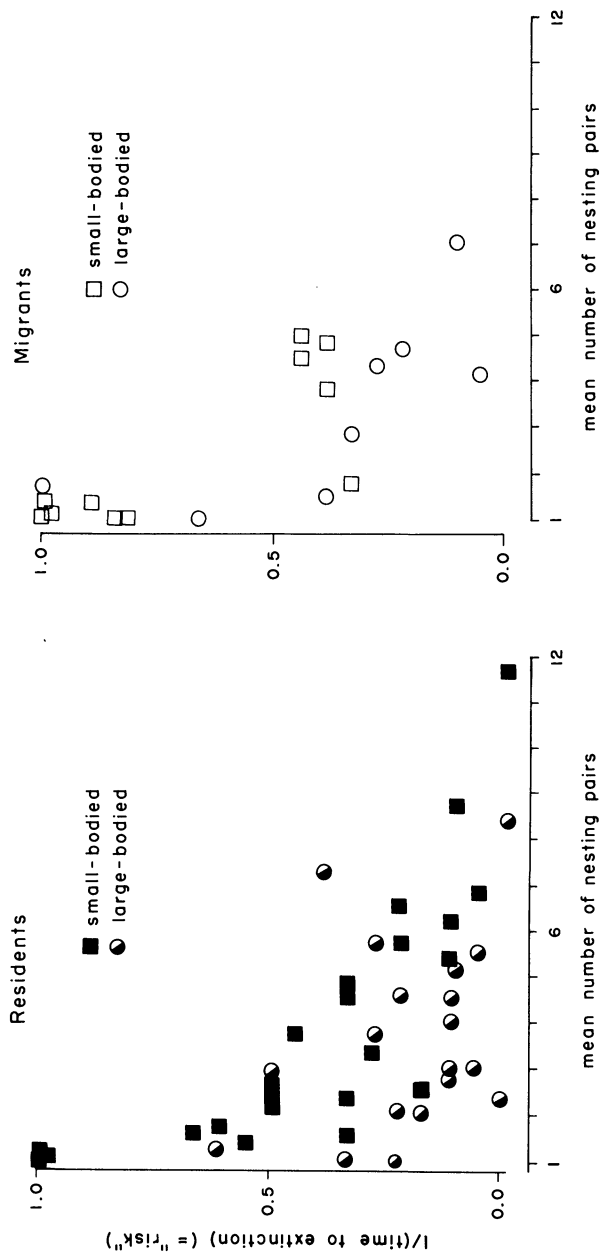


Fig. 3.—Risk of extinction per year (mean reciprocal of time to extinction, in years) for 62 bird species, plotted against mean population size (number of nesting pairs). Risk decreases steeply with population size, but there is much scatter, resulting in part from the factors analyzed in figures 4 and 5.

1.0 per year for the smallest populations of a mean size of one pair to values of less than 0.1 per year for large populations with a mean size over eight pairs. Even though each point summarizes data for populations of a single species on up to 16 islands, the same relationship is obtained if all data are drawn from a single island (cf. Diamond 1984a, fig. 2). A similar relationship has been obtained for breeding bird populations of the California Channel Islands (see Jones and Diamond 1976, fig. 6). Thus, our theoretical prediction 1 is reconfirmed.

Effects Related to Body Size

There is nevertheless much scatter in figure 3, suggesting that species differences in mean population size are not the sole reason for species differences in susceptibility to extinction. As a first step toward understanding this scatter, we analyzed corrected risk of extinction (C) versus population size coded for large- and small-bodied species. The regression lines for large- and small-bodied species differ significantly, both in slope ($P = 0.002$) and in intercept ($P = 0.001$). For small-bodied birds, the correction for population size removes the dependence of the risk of extinction on population size. (That is, the regression slope of C versus N does not differ significantly from zero.) Evidently, for small-bodied species, the times to extinction increase as the power of population size, yielding C independent of N . For large-bodied birds, however, the corrected risk of extinction increases significantly with N ($P = 0.01$), suggesting that times to extinction increase more slowly than the power of population size.

The regression analysis also illustrated that, for a given population size below about seven pairs, a large-bodied species is less prone to extinction than a small-bodied species. For populations above seven pairs, the advantage reverses, and the small-bodied species becomes less prone to extinction. The statistical justifications for this crossover are that for large-bodied species the intercept of the regression line is significantly less than for small-bodied species and that the slope of the regression line is significantly greater for the large-bodied species than for the small-bodied species. Thus, our theoretical predictions 2 and 3 are confirmed.

Effects of Migratory Status

The effects of migratory status (being a migrant versus being a resident) complicate this result but do not alter it. Given the effects of body and population size and the interaction between them, migrants tended to have a significantly ($P = 0.001$) greater corrected risk of extinction. Given this important difference between migrants and residents, we plot their corrected risks of extinction separately in figure 4.

Large-bodied resident species are less prone to extinction than small-bodied ones at low population densities, but the corrected risk of extinction increases much more rapidly with increasing density in large-bodied species (fig. 4; statistical analyses in table 3). This result is the same for the entire data set and confirms predictions 2 and 3.

For migrant species, we do not find these effects. The corrected risk of extinc-

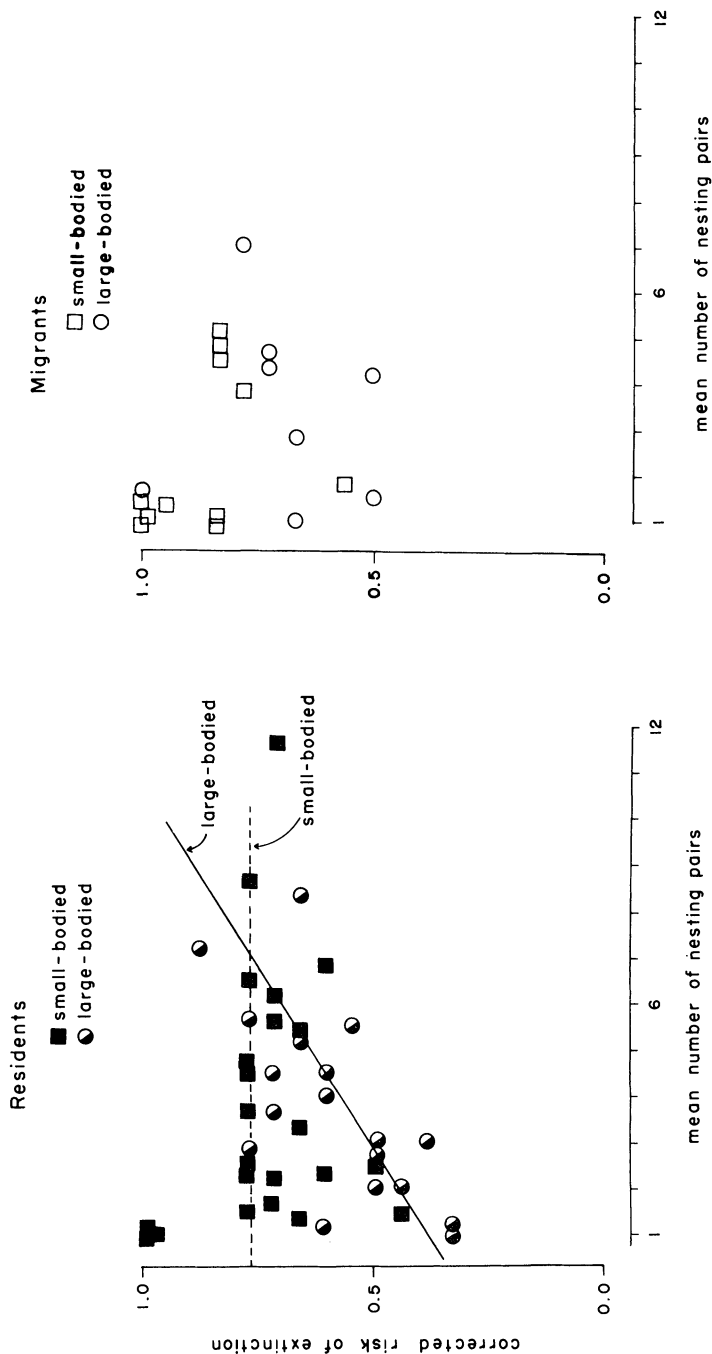


Fig. 4.—Corrected risk of extinction ($C = (1/T)^{1/N}$) plotted against mean population size (N , number of nesting pairs), for species as defined in table 2. For resident species, the two straight lines are the regression lines fitted through the points for large- and small-bodied species. The lines differ significantly in slope and in intercept. The slope for large-bodied species differs significantly from zero; that for small-bodied species does not. The position of the intersection signifies that, for the same population size, a large-bodied species is less prone to extinction than a small-bodied one if the population is small (less than about seven pairs), but more prone than a small-bodied one if the population is large. For migrant species, large- and small-bodied species do not differ significantly and population size has no significant effect. Migrant species, however, have higher corrected risks of extinction than resident species of the same body size and population size. See the text for discussion.

tion does not differ significantly for large- and small-bodied species, and it is not significantly affected by population size (fig. 4; statistical analyses in table 3).

Of course, rather few species are migrants (less than one-third of the 62 species analyzed), and the data span a small range of population sizes. We have already noted that predictions 2 and 3 are still supported if we combine the migrant and resident species.

Species for Which No Extinction Was Recorded

Five species are omitted from figures 3 and 4 because we did not observe any extinction for them. Three are large-bodied species (red grouse, chough, and oystercatcher) with average densities of 1, 4.25, and 10, respectively, and two are small-bodied (twite and rock pipit) with average densities of 4.5 and 7. (These species are all residents, contributing to our conclusion that residents are less prone to extinction than migrants.) On figure 3, values of zero for $1/T$ for these densities do not appear unusual. On figure 4, assigning values of zero for the corrected risks of extinction creates values that are statistical outliers. These five species are not ecologically unusual in any obvious way. They include both large- and small-bodied species, and it seems to us that the most sensible way to treat these points is to exclude them. Giving them corrected risks of extinction of zero would make these values substantial underestimates, particularly at the higher densities (see "Technical Comments").

Effect of Temporal Coefficient of Variation

Having recognized the dependence of the risk of extinction on population size, migratory status, and body size in figures 3 and 4, we can now test for an effect of population variability. Figure 5 plots the residuals from the regression lines of figure 4 (table 2, col. 7) against CV. As shown by the statistical analysis of table 3, temporally variable populations are more prone to extinction (for a given population size and body size) than populations with low temporal variability ($P = 0.05$; table 3). This result confirms our theoretical prediction 4.

DISCUSSION

We compare, in turn, our results for the effects of population size, body size, temporal variability, and migrant or resident status with theoretical predictions and previous results. We conclude by mentioning implications of our study for conservation biology.

Previous Studies of the Effect of Population Size

Our figure 3 confirms directly the theoretical prediction that the risk of extinction should decrease with population size. This effect has been noted in several previous studies that also measured population size directly, as did our study, or else estimated population densities: studies of turnover of Californian island birds (Jones and Diamond 1976), British island birds (Diamond 1984a), and Bahamian island spiders (Toft and Schoener 1983); and studies of relaxation in super-saturated communities of New Zealand land-bridge-island birds, Solomon land-

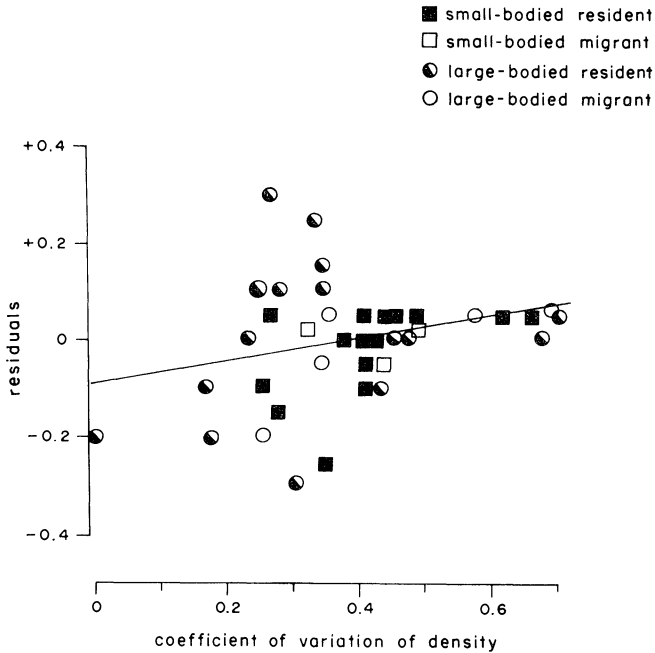


FIG. 5.—*Ordinate*, Residuals from the regression lines through the data of figure 4, which plotted corrected risk of extinction against population size. *Abscissa*, Temporal coefficient of variation in population size. Each point is for one species. Positive or negative residuals mean that a species is, respectively, more or less prone to extinction than one would expect from its population size and body size alone. The slope of a regression line through these residual points is significantly greater than 0, meaning that susceptibility to extinction increases with temporal variability in population size.

bridge-island birds (Diamond 1984a), and birds of Brazilian forest fragments (Willis 1979; Terborgh and Winter 1980). More often, however, the effect of population size on extinction rates has been deduced indirectly in either of two ways. One approach has been to measure the fraction of a fauna's species becoming extinct on islands of different areas, which are assumed to support different mean population sizes. This approach was used in turnover studies of Californian (Jones and Diamond 1976) and British (Diamond 1984a) island birds and in relaxation studies of Asian land-bridge-island mammals (Wilcox 1980), Gulf of California island lizards (Wilcox 1978), North American mountaintop mammals (Brown 1971; Patterson 1984), and Brazilian forest-fragment birds (Willis 1979; Terborgh and Winter 1980). The other indirect approach has been to compare the relative number of extinctions (on the same island) in different groups of species expected to differ in mean population size, such as carnivores versus herbivores or habitat specialists versus generalists (Australian land-bridge-island mammals, Diamond 1984a; North American mountaintop mammals, Brown 1971, Patterson 1984).

These effects of population size on the risk of extinction are sufficiently steep, conspicuous, and ubiquitous that it is difficult to study any other putative predictor of extinction until the effect of population size has been factored out.

Previous Studies of the Effect of Body Size

Several studies have noted that large-bodied species tend to be more prone to extinction than are small-bodied species (Australian land-bridge-island mammals, Diamond 1984a; North American mountaintop mammals, Brown 1971, Patterson 1984; New Guinean land-bridge-island birds, Diamond 1984a). However, these studies did not remove the effect of population size, and undoubtedly the main reason why large animals were found to be prone to extinction is that large animals tend to have lower population sizes.

We derive a new theoretical prediction about the residual effect of body size, once the effect of its correlate of low population size has been removed. Large body size is correlated with longevity and with low rates of increase, which have opposite effects on susceptibility to extinction. The net result is that, for a given population size, small numbers of large species are predicted to be less prone to extinction than small species, but large numbers of large species are predicted to be more prone to extinction. We confirmed this prediction and showed that the crossover population size for British island land birds is around seven pairs.

The theoretical prediction for the crossover population size was five pairs, remarkably close to the crossover estimate of seven pairs that we observe. In view of the uncertainties of the mathematical models, is this apparent agreement merely a coincidence? Leigh's model, on which we based our calculation, assumes only demographic accidents and a rather unusual growth curve. Although both these assumptions may dramatically affect times to extinctions of large populations, their effects on small populations may be minimal. For populations of less than five pairs, demographic accidents are probably the most serious source of density variation, and slight differences in the form of the growth curve have little effect. Hence, the match between the theoretical prediction and the observed result is probably not a coincidence.

Previous Studies of the Effect of Temporal Variability in Population Size

An earlier analysis of the same data base that we used (Diamond 1984a) plotted the risk of extinction against population size on each island, as we did in figure 3 for all islands combined. In this analysis, species with risks of extinction above or below the general trend tended to have high or low temporal variabilities (CV's), respectively. Our figure 5 confirms this impression quantitatively, by first constructing figure 4 to remove much of the effect of mean population size, then plotting the residuals from figure 4 against CV to demonstrate the effect of CV. As far as we are aware, the sole previous demonstration that species with more-variable populations are more prone to extinction was for birds of Barro Colorado Island (Karr 1982). We expect, however, that the effect will prove nearly ubiquitous and will be seen whenever the effect of population size is corrected for.

Previous Studies of the Effect of Migrant or Resident Status

We are not aware of previous studies that compared the risk of extinction for migrant and resident bird species. In our study, migrant species had a greater corrected risk of extinction than did resident species of the same population size and body size. We do not necessarily expect this conclusion to be generalizable to other data sets, since one would expect natural selection to cause a population to evolve whichever status (migrant or resident) maximized individual survival.

Significance for Conservation

Efforts of conservation biologists tend to focus on species that are rare. Rare species may be carnivores, or large-bodied, or habitat specialists, or depleted by human impacts. Figure 3 supports these priorities by showing that small populations are the most prone to extinction. However, field experience illustrates that rare species are not the only threatened ones, even in the absence of human impacts. For example, Lovejoy et al. (1984) were surprised to find that the most abundant nocturnal mammal at their Brazilian forest sites, a spiny rat of genus *Proechimys*, quickly became extinct in isolated forest patches. Note the major effect of population size on *short-term* extinctions (over a period of one or a few decades) of *very small* populations (<10 pairs; fig. 3). Our short-term data base included no extinction of a population with mean numbers over 18 pairs.

The fate of medium-sized populations on a medium time scale may no longer be dominated by population size alone. Instead, the other factors that we analyzed (temporal variability, rate of increase, longevity) may become more important. For example, large-bodied species are at preeminent risk for reasons besides their often-discussed tendency to be rare: figure 4 shows that a moderately numerous population of a large species is at greater risk than even an equally numerous population of a small species. As another example, figure 5 warns us that on-the-average moderately abundant species with very variable numbers may be at greater risk than a rare species with steadier numbers.

Conservation biologists tend to write off as hopeless those species numbering only 7 pairs and to concentrate on saving endangered species reduced to 20–500 pairs, for which there is more hope. Since our “crossover population size,” at which large-bodied and small-bodied species face equal risk, is only 7 pairs, readers may initially view that discovery of a crossover population size as of only academic interest. In fact, such small populations are of practical conservationist concern in numerous situations, including the following. First, the populations and habitats of many endangered species are fragmented, forcing one to consider the viability of many isolated small subpopulations rather than of one contiguous large population. Second, programs of reintroduction to the wild must evaluate whether to reintroduce all 50 available individuals at one site or instead to reintroduce a set of 10 to each of five different sites. The best strategy depends partly on the considerations of this paper. Finally, zoo captive-breeding programs often start out with only a few individuals. Yet, there are far more candidate species for such programs than zoos can accommodate. The considerations of this paper offer zoos

some guidance as to which species offer the best chance of success for surviving the initial demographic bottleneck.

Thus, we hope that improved theoretical understanding of extinctions will offer quantitatively precise criteria for setting priorities in conservation biology.

SUMMARY

Well-known theoretical predictions are that the risk of extinction should decrease with maximum population size (K) and should increase with the temporal coefficient of variation in population size (CV). In an unvarying environment, where extinction is caused solely by demographic accidents, the risk of extinction should decrease steeply with K ; the greater the contribution of environmental variability to the risk of extinction, the less steep should be the dependence on K .

Large-bodied species tend to have long lifetimes but low rates of increase, which have opposite effects on the risk of extinction per year. We show that in comparisons of a large- and small-bodied species at the same average population size (N), the large-bodied species should be at less risk at low N but at greater risk at high N .

We test these predictions using a data base of short-term survivals (up to a few decades) of 355 populations belonging to 100 species of British land birds on 16 islands. The mean N and risk of extinction are known for these populations, and we can calculate CV's for 39 of the species. To identify how factors other than N affect the risk of extinction, we devise a means of correcting that risk for much of the effect of N . We make the following observations.

(1) Risk of extinction does decrease sharply with N . (2) After correcting for much of the effect of N , we confirm the theoretical prediction that the relative susceptibility to extinction of large- and small-bodied species reverses with increasing population size. Above seven pairs, larger-bodied species are at greater risk than smaller-bodied species; the reverse is true below seven pairs. (3) Migratory species are at greater risk of extinction than resident species. (4) Finally, after accounting for the effects of N , body size, and migratory status, we show that the risk of extinction does increase with the CV.

APPENDIX

THE PERSISTENCE TIMES OF BIRD SPECIES ON SMALL ISLANDS OFF THE COAST OF BRITAIN

Order/Species	Island	1/T*	Mean No. Nesting Pairs	CV†
Falconiformes				
Sparrowhawk	Bardsey	0.33	1.0	—
<i>Accipiter nisus</i>				
Buzzard	Lundy	0.30	1.5	—
<i>Buteo buteo</i>	Skokholm	0.25	1.0	—
	Skomer	0.00	3.5	0.23
Kestrel	Bardsey	0.00	1.0	0.00
<i>Falco tinnunculus</i>	Calf	0.25	1.5	—
	Cape Clear	0.10	1.0	0.31
	Handa	1.00	1.0	—
	Lundy	0.11	2.0	0.36
	Skomer	0.25	1.0	—
	St. Agnes	0.00	1.0	0.00
Peregrine	Cape Clear	1.00	1.0	—
<i>F. peregrinus</i>	Fair	0.15	1.5	0.34
	Handa	1.00	1.0	—
	Lundy	0.23	1.0	0.33
Galliformes				
Red grouse	Handa	0.00	1.0	—
<i>Lagopus lagopus</i>				
Pheasant	Havergate	0.00	16.0	0.39
<i>Phasianus colchicus</i>	Lundy	0.04	3.0	0.40
	Scolt Head	1.00	1.0	—
	Skokholm	—	—	0.27
	Skomer	0.00	2.5	—
Partridge	Calf	0.00	7.0	0.68
<i>Perdix perdix</i>	Havergate	0.17	4.0	—
	Scolt Head	0.17	4.5	—
Red-legged partridge	Havergate	0.17	2.0	—
<i>Alectoris rufa</i>	Scolt Head	0.09	3.5	—
Quail	Fair	0.67	1.0	—
<i>Coturnix coturnix</i>				
Gruiformes				
Water rail	Copeland	0.06	3.0	—
<i>Rallus aquaticus</i>				
Corncrake	Bardsey	0.50	2.0	—
<i>Crex crex</i>	Cape Clear	0.00	9.5	0.70
	Fair	0.21	2.5	—
Moorhen	Bardsey	0.00	3.5	0.66
<i>Gallinula chloropus</i>	Calf	0.00	1.5	0.36
	Cape Clear	0.00	3.5	0.42
	Copeland	0.00	11.5	0.58
	Farne	0.50	1.0	—
	Havergate	0.00	11.0	0.40
	Skokholm	0.25	1.0	—
	Skomer	0.11	2.5	—
	St. Agnes	0.25	1.0	—
Coot	St. Agnes	0.20	1.0	—
<i>Fulica atra</i>				
Charadriiformes				
Oystercatcher	Bardsey	—	—	0.20

APPENDIX (Continued)

Order/Species	Island	1/T*	Mean No. Nesting Pairs	CV†
<i>Haematopus ostralegus</i>	Calf	0.00	12.5	0.25
	Cape Clear	0.00	15.0	0.48
	Copeland	0.00	13.0	0.56
	Fair	0.00	5.0	—
	Farne	—	—	0.33
	Hascosay	—	—	0.38
	Havergate	0.00	4.5	0.33
	Lundy	0.00	13.0	0.42
	May	0.00	14.5	0.11
	Scolt Head	0.00	6.7	0.30
	Skokholm	—	—	0.08
	Skomer	—	—	0.18
	St. Agnes	0.00	7.0	0.34
	Bardsey	0.00	8.5	0.48
Lapwing	Calf	0.00	8.0	—
<i>Vanellus vanellus</i>	Copeland	0.10	4.0	0.51
	Fair	0.13	6.5	0.73
	Farne	0.33	2.0	—
	Handa	0.33	2.5	—
	Hascosay	0.17	16.5	—
	Havergate	0.20	1.0	—
	Lundy	0.00	15.0	0.57
	Scolt Head	0.27	4.5	—
	Skokholm	0.00	13.0	0.61
	Skomer	0.11	2.0	—
	Fair	1.00	1.0	—
	Handa	1.00	2.0	—
	Hascosay	1.00	2.0	—
	Bardsey	0.00	1.0	—
Ringed plover	Copeland	0.30	2.0	0.37
<i>Charadrius hiaticula</i>	Fair	0.00	3.5	0.67
	Farne	0.00	14.0	0.25
	Handa	0.00	3.5	—
	Hascosay	0.00	5.5	0.41
	Havergate	0.00	5.0	0.68
	Scolt Head	—	—	0.27
	St. Agnes	0.00	10.0	0.30
	Bardsey	0.17	1.0	—
	Calf	0.25	1.5	—
	Fair	0.75	1.0	—
Curlew	Hascosay	0.50	2.0	—
	Lundy	0.25	1.0	—
	Skomer	0.00	10.5	0.35
	Farne	1.00	1.0	—
	Hascosay	0.00	2.0	—
Redshank	Havergate	0.00	10.5	0.19
	Scolt Head	0.00	4.0	0.54
	Cape Clear	0.00	8.0	0.26
	Fair	0.00	2.0	—
<i>Gallinago gallinago</i>	Handa	0.00	3.5	—
	Hascosay	0.25	3.0	—
Columbiformes				
Rock dove	Cape Clear	—	—	0.29

(continued)

APPENDIX (Continued)

Order/Species	Island	1/T*	Mean No. Nesting Pairs	CV†
<i>Columba livia</i>	Fair	0.08	8.0	—
	Handa	0.00	3.0	—
	Hascosay	0.00	14.0	0.07
Stock dove	Calf	0.00	1.0	—
<i>C. oenas</i>	Cape Clear	0.22	3.5	—
	Copeland	0.00	5.5	0.34
	Farne	1.00	1.0	—
	Scolt Head	0.50	1.0	—
	Skomer	0.00	10.0	—
Wood pigeon	Bardsey	0.50	1.0	—
<i>C. palumbus</i>	Calf	0.00	1.0	—
	Cape Clear	0.00	4.0	—
	Lundy	0.18	2.0	—
	Scolt Head	0.14	7.0	—
	Skomer	0.00	1.5	—
Cuculiformes				
Cuckoo	Bardsey	0.60	1.0	—
<i>Cuculus canorus</i>	Calf	1.00	1.0	—
	Cape Clear	0.17	2.5	—
	Lundy	0.30	1.5	—
	May	0.00	1.5	—
	Scolt Head	0.60	1.0	—
	Skomer	0.50	1.0	—
	St. Agnes	0.00	2.0	—
Strigiformes				
Short-eared owl	Calf	0.17	1.5	—
<i>Asio flammeus</i>	Havergate	0.14	2.5	0.70
	Scolt Head	0.55	1.0	—
	Skomer	0.11	3.0	—
Little owl	Bardsey	0.00	4.5	0.27
<i>Athene noctua</i>	Skomer	1.00	1.0	—
Passeriformes				
Skylark	Bardsey	0.07	5.0	0.35
<i>Alauda arvensis</i>	Calf	0.00	5.5	0.56
	Cape Clear	—	—	0.91
	Hascosay	0.00	13.0	0.31
	Havergate	0.00	14.5	0.29
	Hilbre	0.15	2.5	0.20
	Scolt Head	0.00	1.6	—
	Skokholm	—	—	0.44
	St. Agnes	0.00	6.0	0.25
Swallow	Bardsey	0.00	5.5	0.30
<i>Hirundo rustica</i>	Calf	0.00	3.0	0.49
	Cape Clear	0.00	16.0	—
	Copeland	0.50	2.0	—
	Fair	1.00	1.0	—
	Havergate	0.25	2.5	—
	Hilbre	0.75	1.0	—
	Lundy	0.75	1.0	—
	May	—	—	0.45
	Scolt Head	0.42	1.0	—
	Skokholm	1.00	1.0	—
	Skomer	0.00	4.0	—

APPENDIX (Continued)

Order/Species	Island	1/T*	Mean No. Nesting Pairs	CV†
	St. Agnes	0.00	8.0	—
House martin	Cape Clear	0.14	6.5	—
<i>Delichon urbica</i>	Farne	1.00	6.0	—
	Skomer	0.25	2.5	—
Yellow wagtail	Havergate	1.00	1.0	—
<i>Motacilla flava</i>	Scolt Head	1.00	1.5	—
Pied wagtail	Bardsey	0.09	2.5	0.20
<i>M. alba</i>	Cape Clear	0.00	11.5	—
	Copeland	0.33	1.0	—
	Fair	1.00	1.0	—
	Farne	0.25	1.0	—
	Handa	1.00	1.0	—
	Hilbre	0.11	1.5	0.36
	Lundy	0.36	1.5	—
	May	0.17	2.0	0.30
	Skokholm	0.40	1.0	—
	Skomer	0.00	1.0	0.28
Meadow pipit	Bardsey	—	—	0.39
<i>Anthus pratensis</i>	Calf	—	—	0.47
	Farne	0.50	1.5	—
	Hascosay	0.00	4.5	—
	Havergate	0.00	12.5	0.48
	Hilbre	0.00	6.5	0.34
	May	0.13	5.5	0.56
	Scolt Head	0.00	1.6	—
	Skokholm	—	—	0.22
Rock pipit	Bardsey	—	—	0.37
<i>A. spinoletta</i>	Calf	—	—	0.23
	Copeland	0.00	7.5	0.41
	Farne	—	—	0.38
	Hascosay	0.00	7.0	0.23
	May	—	—	0.31
	Skokholm	—	—	0.18
Wren	Bardsey	—	—	0.39
<i>Troglodytes troglodytes</i>	Calf	—	—	0.66
	Cape Clear	—	—	0.82
	Handa	0.00	4.0	—
	Hascosay	0.20	5.0	—
	Lundy	0.00	8.0	—
	Skomer	0.25	7.5	—
Dunnock	Bardsey	0.00	15.5	0.40
<i>Prunella modularis</i>	Calf	0.00	12.0	0.55
	Copeland	0.00	2.5	0.25
	Havergate	0.17	3.5	—
	Hilbre	1.00	1.0	—
	Lundy	0.00	7.0	0.61
	May	0.20	2.0	—
	Scolt Head	0.00	1.5	—
	Skokholm	0.00	4.0	0.35
	Skomer	0.00	12.0	0.28
Robin	Bardsey	0.23	3.0	—
<i>Erithacus rubecula</i>	Calf	0.10	3.5	—
	Cape Clear	—	—	0.30
	Farne	1.00	1.0	—

(continued)

APPENDIX (Continued)

Order/Species	Island	1/T*	Mean No. Nesting Pairs	CV†
Stonechat <i>Saxicola torquata</i>	Hascosay	0.00	1.0	—
	Lundy	0.00	6.0	0.22
	St. Agnes	0.17	5.5	—
	Bardsey	0.07	7.0	0.49
	Calf	0.17	9.0	—
	Farne	1.00	1.0	—
	Handa	0.50	1.5	—
	Lundy	0.50	2.5	—
	Skomer	0.50	2.0	—
	St. Agnes	0.20	2.5	—
Wheatear <i>Oenanthe oenanthe</i>	Bardsey	0.00	9.5	0.63
	Calf	0.20	4.5	—
	Farne	0.67	1.0	—
	Hascosay	0.00	13.5	0.21
	Havergate	1.00	1.0	—
	Lundy	0.00	5.5	0.30
	May	0.08	5.5	—
	Scolt Head	1.00	2.0	—
	Skomer	—	—	0.17
	St. Agnes	0.50	1.0	—
Blackbird <i>Turdus merula</i>	Bardsey	0.00	14.5	1.04
	Calf	0.00	9.5	0.61
	Cape Clear	—	—	0.29
	Copeland	0.00	6.0	0.40
	Fair	0.60	1.5	—
	Farne	0.09	1.5	0.52
	Hascosay	—	—	0.00
	Havergate	1.00	1.0	—
	Hilbre	0.06	2.0	0.45
	Lundy	0.00	13.0	0.08
	May	0.07	1.5	0.55
	Scolt Head	0.75	1.0	—
	Skokholm	1.00	1.0	—
	Skomer	0.12	3.5	—
	Bardsey	0.40	2.0	—
Song thrush <i>T. philomelos</i>	Calf	0.50	1.5	—
	Copeland	0.75	1.5	—
	Lundy	0.29	1.5	—
	Skomer	1.00	2.0	—
	Calf	0.00	1.0	—
Mistle thrush <i>T. visvivorus</i>	Cape Clear	0.67	2.0	—
	Scolt Head	1.00	1.0	—
	Calf	1.00	1.0	—
Grasshopper warbler <i>Locustella naevia</i>	Skomer	0.67	1.0	—
	Bardsey	0.33	1.0	—
	Calf	0.67	1.0	—
	Cape Clear	0.10	4.0	—
	Copeland	0.33	1.5	—
	Skomer	0.14	2.0	—
	Bardsey	0.07	8.0	0.44
Sedge warbler <i>Acrocephalus schoenobaenus</i>	Calf	0.27	2.5	0.47
	Copeland	1.00	3.0	—
	Lundy	0.30	2.0	—
	Skokholm	1.00	1.0	—
	Skomer	0.00	10.0	0.52
Whitethroat <i>Sylvia communis</i>				

APPENDIX (Continued)

Order/Species	Island	1/T*	Mean No. Nesting Pairs	CV†
Willow warbler	Bardsey	1.00	1.0	—
<i>Phylloscopus trochilus</i>	Lundy	0.80	1.5	—
Chiffchaff	Lundy	1.00	1.0	—
<i>P. collybita</i>				
Goldcrest	Lundy	1.00	1.0	—
<i>Regulus regulus</i>				
Spotted flycatcher	Calf	1.00	1.0	—
<i>Muscicapa striata</i>	Lundy	0.25	1.0	—
	Skomer	1.00	1.0	—
	St. Agnes	1.00	1.0	—
Pied flycatcher	Havergate	1.00	1.0	—
<i>Ficedula hypoleuca</i>				
Great tit	Cape Clear	0.33	1.0	—
<i>Parus major</i>	St. Agnes	0.00	4.0	0.35
Blue tit	Cape Clear	0.13	2.0	—
<i>P. caeruleus</i>	St. Agnes	0.50	1.0	—
Yellowhammer	Bardsey	0.00	3.0	0.20
<i>Emberiza citrinella</i>	Cape Clear	—	—	0.56
	Lundy	1.00	2.0	—
Reed bunting	Bardsey	0.09	2.5	0.47
<i>E. schoeniclus</i>	Calf	0.00	5.0	0.88
	Cape Clear	0.10	9.0	—
	Havergate	0.17	3.0	—
	Lundy	1.00	1.0	—
	Scolt Head	0.09	18.0	—
	Skokholm	0.13	2.5	—
	Skomer	0.00	4.0	—
Chaffinch	Bardsey	1.00	1.0	—
<i>Fringilla coelebs</i>	Calf	1.00	1.0	—
	Lundy	0.00	5.5	0.42
	St. Agnes	0.07	2.0	—
Goldfinch	Lundy	0.67	1.5	—
<i>Carduelis carduelis</i>				
Siskin	Lundy	1.00	1.0	—
<i>C. spinus</i>				
Redpoll	Copeland	1.00	1.0	—
<i>Acanthis flammea</i>				
Twite	Handa	0.00	4.0	—
<i>A. flavirostris</i>	Hascosay	0.00	5.0	—
Linnet	Bardsey	—	—	0.30
<i>A. cannabina</i>	Calf	0.00	8.5	0.68
	Havergate	0.00	10.0	0.17
	Hilbre	0.08	2.5	0.60
	Lundy	0.09	17.5	—
	May	0.20	4.5	—
	Scolt Head	0.00	1.5	—
	Skomer	1.00	1.0	—
House sparrow	Bardsey	—	—	0.38
<i>Passer domesticus</i>	Calf	0.50	1.0	—
	Hascosay	0.00	5.0	0.17
	Havergate	1.00	2.5	—
	Hilbre	0.00	2.5	—
	Lundy	0.00	15.0	—
	Skomer	0.50	1.0	—

(continued)

APPENDIX (Continued)

Order/Species	Island	1/T*	Mean No. Nesting Pairs	CV†
Tree sparrow	Copeland	1.00	3.0	—
<i>P. montanus</i>	Fair	0.25	2.0	—
	Lundy	0.33	1.5	—
Starling	Bardsey	—	—	—
<i>Sturnus vulgaris</i>	Calf	—	—	0.31
	Copeland	0.00	15.0	0.42
	Farne	0.00	6.0	0.51
	Hascosay	—	—	0.33
	Hilbre	0.07	6.5	0.36
	May	0.00	12.5	—
	Skokholm	0.00	17.0	0.53
	Skomer	0.12	5.5	—
	St. Agnes	0.00	12.0	—
Magpie	Calf	0.00	4.0	0.45
<i>Pica pica</i>	Cape Clear	0.00	11.0	0.33
	Copeland	0.07	1.5	0.59
	Skomer	0.33	1.5	—
Chough	Bardsey	0.00	2.5	0.38
<i>Pyrrhocorax pyrrhocorax</i>	Calf	0.00	5.5	0.34
	Cape Clear	0.00	7.5	0.31
	Skomer	0.00	2.0	0.10
Jackdaw	Bardsey	—	—	0.32
<i>Corvus modelula</i>	Copeland	0.00	9.5	0.42
	Fair	1.00	1.0	—
	Farne	0.50	2.0	—
	Skokholm	0.00	16.0	—
	Skomer	—	—	0.10
Carriion crow or	Bardsey	0.00	4.5	0.25
Hooded crow	Calf	0.00	5.5	0.26
<i>C. corone</i>	Cape Clear	0.00	13.0	—
	Copeland	0.00	1.0	—
	Fair	0.00	10.5	—
	Handa	0.00	3.5	—
	Hascosay	0.00	4.5	0.22
	Havergate	1.00	1.0	—
	Hilbre	0.33	1.0	—
	Lundy	0.00	5.5	0.30
	May	0.50	1.0	—
	Scolt Head	1.00	1.0	—
	Skokholm	0.00	7.5	0.20
	Skomer	—	—	0.21
Raven	Bardsey	0.00	2.0	0.41
<i>C. corax</i>	Calf	0.08	1.0	0.28
	Cape Clear	0.09	1.0	—
	Fair	0.00	3.0	0.27
	Handa	0.00	2.0	—
	Hascosay	0.00	1.5	0.38
	Lundy	0.00	4.0	0.39
	Skokholm	0.00	1.0	0.12
	Skomer	0.00	4.0	0.27

NOTE.—The species are grouped by taxonomic order. See the section on “Data Preparation” for an explanation of columns 3–5.

* T, Time to extinction.

† CV, Temporal coefficient of variation in density.

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